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The hermaphroditic sea anemone *Anthopleura atodai* n. sp. (Anthozoa: Actiniaria: Actiniidae) from Japan, with a redescription of *A. hermaphroditica*

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Abstract.—A new species of internally brooding sea anemone, *Anthopleura atodai,* is described from the middle to northern Pacific coasts of Honshu, Japan. This species attaches to mussels or in rock crevices of the higher tidal zone. This is the second hermaphroditic species and fourth internally brooding species of *Anthopleura* to be reported; it is distinguished from other members of *Anthopleura* by a combination of the following features: brooding its young, synchronously hermaphroditic, S-shaped basitrichs in filaments, 40 to 68 tentacles, verrucae in the proximal part of the column larger than those in the distal part, cobalt-blue spot at the distal end of each siphonoglyph. *Anthopleura hermaphroditica,* the species that most closely resembles *A. atodai,* is redescribed to clearly differentiate it from *A. atodai* and to resolve questions about its taxonomy and identity.

Anthopleura Duchassaing and Michelotti, 1861, one of the largest genera in the Actiniaria, includes about 50 species (Carlgren 1949; Dunn 1974, 1978, 1982a; Fautin 2003). In Japanese waters, six species of *Anthopleura* are known: *Anthopleura asiatica* Uchida & Muramatsu, 1958; *A. fuscoviridis* Carlgren, 1949; *A. kurogane* Uchida, 1938; *A. mcmurrichi* Wassilieff, 1908; *A. pacifica* Uchida, 1938; *A. uchidai* England, 1992. Additionally, Atoda (1954) reported the post-larval development of an unidentified species of *Anthopleura,* which broods its young in the colenteron. Although Atoda (1954) mentioned that the species could be distinguished from other species of *Anthopleura* by its coloration, it has never named; we formally describe it here as a new species, *A. atodai.*

Internal brooding is widely known in the Actiniaria: e.g. *Actinia* spp. (Chia & Rostron 1960; Rossi 1971; Black & Johnson 1979; Ayre 1983; Manuel 1988; Russo et al. 1994; Yanagi et al. 1996, 1999), *Aulactinia* sp. (Dunn et al. 1980), *Cereus pedunculatus* (Rossi 1971), *Cnidopus japonicus* (T. Uchida 1934, T. Uchida & Iwata 1954), *Epiactis* spp. (Dunn 1975, Fautin & Chia 1986, Edmands 1995), and *Bunodactis hermaphroditica* (McMurrich 1904). Aside from *A. atodai,* three species of Anthopleura are reported to brood internally: *A. handi* Dunn, 1978, from the Philippines, Hong Kong, and Malaysia (Dunn 1978, England 1987); *A. aureoradiata* (Stuckey, 1909a) from New Zealand (Stuckey 1909a, 1909b; Carlgren 1949, 1954; Parry 1951); and *A. hermaphroditica* (Carlgren, 1899) from Chile (Carlgren 1899, 1927, 1949, 1959).

Anthopleura atodai most closely resembles *A. hermaphroditica.* Because the anatomy and cnidom of *A. hermaphroditica* is incompletely known, and its taxonomic status is unclear, we redescribe it to clearly

Fig. 1. Distribution of *Anthopleura atodai,* new species. Stars indicate records of *Anthopleura* sp. given by Atoda (1958); circles indicate sites visited in this study.

distinguish *A. hermaphroditica* from *A. atodai* and to evaluate the proposed synonymy between *A. hermaphroditica* and *A. handi.* We find that *A. hermaphroditica* and *A. atodai* can be distinguished based on color, number of tentacles, cnidom, and geographic range, and that *A. hermaphroditica* is distinct from *A. handi.*

Materials and Methods

Specimens of *Anthopleura atodai* were collected from high intertidal rocky shore around Asamushi (40°54′N, 140°51′E), Otsuchi (39°22′N, 141°58′E), Katsuura (35°07′N, 140°16’ E), and Tateyama (34°58′N, 139°46′E) (Fig. 1). Anatomical observations were made on 17 specimens of *A. atodai*; histological sections were made from 11 specimens. Anatomical observations were made on 10 preserved specimens of *A. hermaphroditica;* histological sections were made from 5 animals. For specimens of both *A. atodai* and *A. hermaphroditica,* histological sections 6–8 μm thick were stained with hematoxylin and eosin or with Haidenhain's Azan (Presnell and Schreibman, 1997).

Cnidae data were gathered following the method of England (1987) and Williams (1996). Cnidae were measured from both live and preserved specimens of *A. atodai,* and from preserved specimens of *A. hermaphroditica.* Cnidae were measured in smash preparations at 1000 X using differential interference light microscopy. The terminology for cnidae follows Weill (1934), Mariscal (1974), and England (1991).

The material examined was deposited in the Costal Branch of Natural History Museum and Institute, Chiba (CMNH), National Science Museum, Tokyo (NSMT), Swedish Museum Natural History, Stockholm (SMNH), State Zoological Museum, Munich (ZSM), and The University of Kansas Natural History Museum and Biodiversity Research Center (KUMNH).

Systematic Account

Family Actiniidae Rafinesque, 1815
Genus *Anthopleura* Duchassaing and Michelotti, 1860
Anthopleura atodai, new species
Figs. 2–5

Anthopleura sp.—Atoda, 1954: 274, figs. 1–29, pls. 6–7.—Isomura et al., 2003: 293, fig. 1.

Holotype.—Kenashi-jima, Otsuchi, Iwate Pref., Honshu, Japan (39°21′30″N, 141°57′50″E), 14 July 1997, collected by KY, 1 specimen, with histological sections and cnidae preparations (CMNH-ZG 64).

Paratypes.—All from Honshu, Japan and collected by KY: Kenashi-jima, Otsuchi, Iwate Pref., 14 Jul 1997, 1 specimen with cnidae preparations (CMNH-ZG 65), 1 specimen with histological sections (NSMT-Co 1373), 1 specimen (NSMT-Co 1374), 1 specimen (KUMNH 1808), 1 specimen entirely sectioned longitudinally (CMNH-ZG 3692), 1 specimen entirely sectioned transversely (CMNH-ZG 3693); Banda, Tateyama, Chiba Pref., 28 Oct 1996, 1 specimen with cnidae preparations

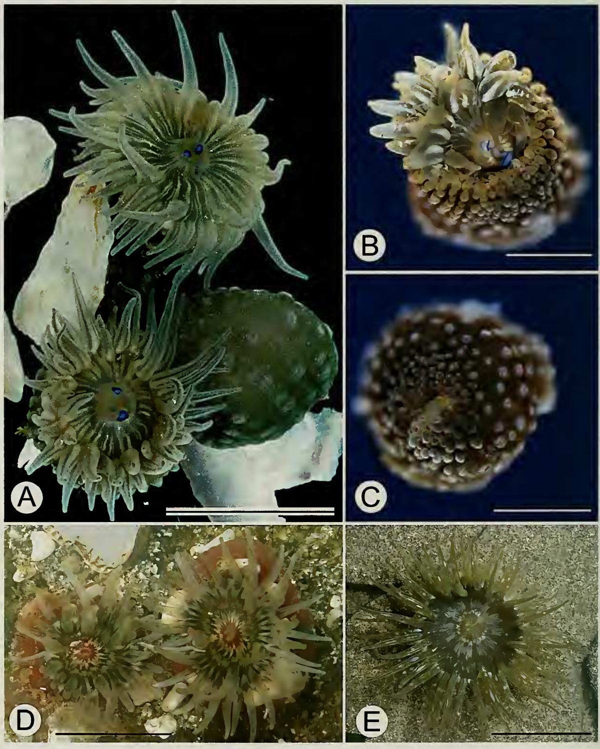

Fig. 2. A–C, Photographs of *Anthopleura atodai,* new species (A, collected at Banda, 24 Feb 1997; B, C, collected at type locality, Kenashi-jima, 14 Jul 1997): A, 2 specimens expanded and 1 specimen contracted; B, semi-expanded specimen; C, fully contracted specimen. D, E, Photographs of *A. hermaphroditica* (collected from Chiloe Island, Chile): D, Two specimens expanded; E, Typical oral disc patterning. Photographs in D, E courtesy of V. Häussermann. Scale Bars: A, D = 10 mm; B, C = 5 mm, E = 20 mm.

(CMNH-ZG 115), 1 specimen (CMNH-ZG 200), 11 Dec 1996, 24 Feb 1997, 1 specimen with cnidae preparations (CMNH-ZG 44), 1 specimen (NSMT-Co 1372), 5 Dec 1997, 1 specimen entirely sectioned longitudinally (CMNH-ZG 3695), 1 specimen entirely sectioned transversely (CMNH-ZG 3696); Hadaka-jima, Asamushi, Aomori Pref., 22 Jun 1998, 1 specimen with histological sections and cnidae preparations (CMNH-ZG 209), 1 specimen with cnidae preparations (CMNH-ZG 210), 1 specimen (KUMNH 1809), 1 specimen entirely sectioned transversely (CMNH-ZG 3697).

Non-type material examined.—All specimens collected from Honshu, Japan by KY: Kedo-ura, Katsuura, Chiba Pref., 1 May 1999, 4 specimens (CMNH-ZG 253); Banda, Tateyama, Chiba Pref., 11 Dec 1996, 4 specimens (CMNH-ZG 201), 24 Feb 1997, 6 specimens (CMNH-ZG 3694), 15 May 2000, 2 specimens (CMNH-ZG 906); Nojima, Otsuchi, Iwate Pref., 8 Aug 2001, 4 specimens (CMNH-ZG1060), 4 specimens (CMNH-ZG 1061); Hadaka-jima, Asamushi, Aomori Pref., 22 Jun 1998, 60 specimens (CMNH-ZG 3698), 5 specimens (KUMNH 1809–1810), 3 specimens (NSMT-Co 1375–1378).

Description.—Column and pedal disc: Freshly collected specimens brown or bluish-green, proximal verrucae whitish (Fig. 2A–C). In living, expanded animals, column width 6–12 mm, almost equal to height (Fig. 2A–C); oral and pedal disc of almost equal width. Column of contracted animals dome-like (Fig. 2A, C). Adhesive endocoelic verrucae in regular vertical rows from margin to limbus; in some individuals, becoming dense and irregular distally (Fig. 2B); number of rows 24–39 (37 in holotype) distally, 24 proximally. Diameter of verrucae increases proximally: 0.4 mm at margin, 0.6–1.2 mm at limbus. In life, verrucae hold bits of gravel and broken shells. Marginal endocoels bear 9–32 pale, opaque, spherical acrorhagi that curve into fosse (Table 1). Pedal disc weakly adherent,

Table 1.—Morphological variability of 11 specimens of *Anthopleura atodai,* n. sp. collected from three localities. "—" indicates that an attribute was not measured or counted for that specimen.

Specimen	Diameter of pedal disc (in mm)	Height of column (in mm)	Number of acrorhabi	Number of pairs of mesenteries		Number of pairs of directive mesenteries	Number of siphonoglyphs
				Distal column	Proximal column		
holotype (CMNH-ZG 64)	12.0	10.7	32	28	28	2	2
paratype (CMNH-ZG 65)	12.4	9.7	23	28	28	2	2
paratype (NSMT-Co 1373)	10.0	14.4	—	34	34	2	2
paratype (KUMNH 1808)	11.7	11.9	—	34	34	2	2
paratype (CMNH-ZG 3693)	—	—	—	39	39	2	2
paratype (CMNH-ZG 209)	9.3	12.1	14	24	24	2	2
paratype (KUMNH 1808)	6.1	7.9	8	20	20	2	2
paratype (CMNH-ZG210)	9.5	9.8	15	28	28	2	2
paratype (CMNH-ZG44)	11.8	9.7	11	38	38	2	2
paratype (CMNH-ZG115)	7.8	11.9	9	34	34	2	2
paratype (CMNH-ZG 3696)	—	—	11	35	35	2	2

circular in outline, paler in color than column.

Oral disc and tentacles: Diameter of oral disc of slightly contracted, fixed anemone approximately equal to that of pedal disc and column. Center of oral disc somewhat elevated into oral cone that bears mouth; mouth elongate along directive axis. Each siphonoglyph marked with a bright cobalt-blue spot in life (Fig. 2A, B); color fades in preservation. Tentacles marginal, slender, shorter than oral disc diameter, number 40 to 62 (59 in holotype). Each tentacle translucent whitish to gray, with parallel longitudinal grayish streaks and/or white flecks on oral surface (Fig. 2A, B). Circular muscles of tentacles endodermal, longitudinal muscles of tentacles ectodermal (Fig. 3B). Numerous zooxanthellae in endoderm.

Marginal sphincter muscle: Endodermal, circumscribed-pinnate to circumscribed-diffuse, with highly branched mesogleal processes (Fig. 4B, C).

Mesenteries and internal anatomy: Actinopharynx whitish, half to two-thirds length of column, with two siphonoglyphs each attached to a pair of directive mesenteries. Distinct marginal stomata; oral stomata not seen. Mesenteries in 24–39 pairs, arranged hexamerously in three to four cycles, same number proximally and distally (Table 1). Mesentery arrangement irregular in specimens that have regeneration scars. All older mesenteries, including directives, fertile; all specimens hermaphroditic, with gametes of both sexes on same mesenteries or not (Fig. 3C). Zooxanthellae more numerous in endoderm of column than in endoderm of mesenteries. Each specimen may contain as many as 22 brooded young, early embryos through young adults with two cycles of mesenteries and tentacles (Fig. 3D–F); brooded young posses zooxanthellae.

Mesenterial retractor muscles strong, diffuse to restricted (Fig. 4A). Parietobasilar muscles well developed, extend half to entire distance between column wall and retractor muscle, with small free pennon distally (Fig. 4A). Basilar muscles distinct (Fig. 3A). Cnidom: Spirocysts, basitrichs, holotrichs, heterotrichs, microbasic *p*-mastigophores, microbasic *p*-amastigophores (Fig. 5). Sizes and distribution of cnidae given in Table 2.

Distribution and habitat.—Known from the middle to northern Pacific coasts of Honshu, Japan (Fig. 1). Found in high intertidal, attached to *Mytilus* or in crevices of rock. Typically forms dense populations.

Etymology.—The species is named after Dr. K. Atoda, who first identified this as a new species.

Anthopleura hermaphroditica (Carlgren, 1899)
Figs. 2, 5, 6

Bunodes hermaphroditicus Carlgren, 1899: 23.

Anthopleura hermaphroditica Carlgren, 1899.—Carlgren 1927: 32.—England 1987: 245.

Anthopleura hermafroditica Carlgr. Carlgren 1949: 54.—1959: 22.

non *Cribrina hermaphroditica* Carlgren, 1899.—McMurrich, 1904: 287.—Dawson, 1992: 38.

Material examined.—SMNH 1177 (syntype), SMNH 40829, 40830; ZSM (unnumbered)

Description.—Column and pedal disc: Freshly collected specimens olive green to rosy pink, proximal verrucae paler (Fig. 2D). In living, expanded specimens, column width 15–20 mm, height 17–25 mm. In contraction, column dome-like, width 4–10 mm, height 3–12.5 mm. Adhesive, endocoelic verrucae (Fig. 6A) in regular vertical rows from margin to limbus; number of rows 23–42. Verrucae larger and more prominent distally than proximally; maximum diameter of distal verrucae 0.5 mm in preserved specimens. In life, verrucae hold small stones and pieces of shells. Margin denticulate, with endocoelic conical projections that bear 1–3 verrucae on the outer surface; projection may bear a swollen acrorhagus on the inner surface. Acrorhagi

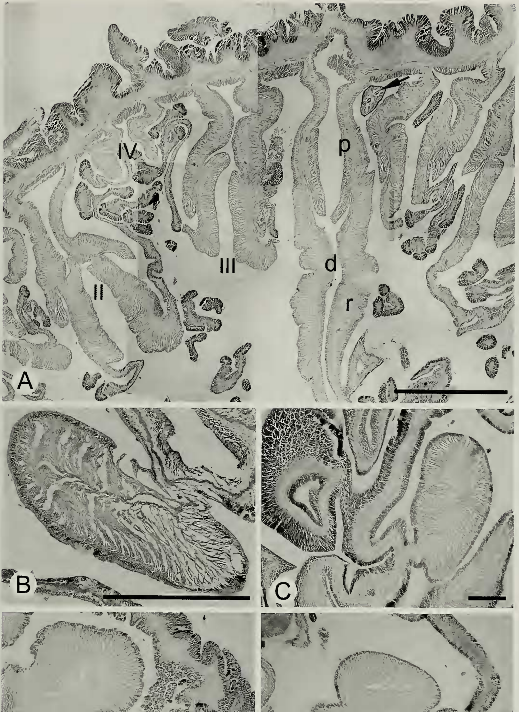

Fig. 3. *Anthopleura atodai,* new species (A, B, holotype CMNH-ZG 64; C, paratype CMNH-ZG NSMT-Co 1373; D, paratype CMNH-ZG 3692; E, paratype CMNH-ZG 3695): A, cross section of proximal column showing directive mesenteries flanked by those of the second (II), third (III) and fourth (IV) cycles; B–E, cross sections thorough circumscribed marginal sphincter. Scale Bars: A = 1 mm; B–E = 200 μm. Abbreviations.—d, directive mesentery; p, parietobasilar muscle; r, retractor muscle. Arrow indicating brooded young.

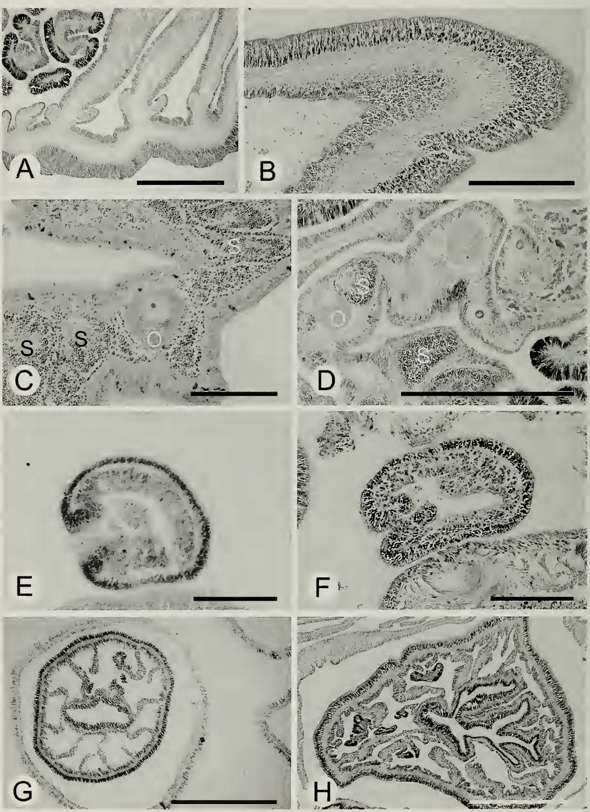

Fig. 4. *Anthopleura atodai,* new species (A, E, paratype CMNH-ZG 3692; B–C, holotype CMNH-ZG 64; D, paratype CMNH-ZG 3969; G, paratype CMNH-ZG 3696; H, paratype CMNH-ZG 209): A, longitudinal section through pedal disc showing basilar muscles; B, longitudinal section through a tentacle; C–D, cross sections through a mesentery showing both spermatocysts and oocytes; E–H, internally brooded young in the enteron (E, F, H), and tentacles (G). Scale Bars: A, C, D = 200 μm; B, G, H = 500 μm; E, F = 100 μm (E–F, Abbreviations.—o, oocyte; s, spermatocysts.

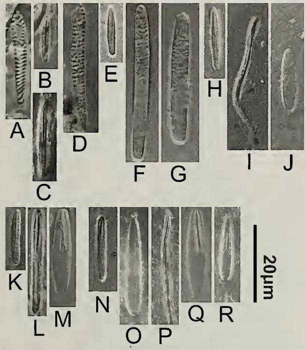

Fig. 5. Cnidae of *Anthopleura atodai*, new species (paratype CMNH-ZG65); see Table 2 for size ranges. The cnidae of *A. hermaphroditica* are identical in morphology and in distribution in the body, but differ in size; see Table 3 for sizes. A-C from tentacles, D-G from acrorhagus, H-J from column, K-M from actinopharynx, N-R from filaments. A, spirocyst; B, basitrich-1; C, basitrich-2; D, spirocyst; E, basitrichs; F, Holotrich; G, Holotrich; H, basitrich-1; I, S-basitrich; J, heterotrich; K, basitrich-1; L, basitrich-2; M, microbasic *p*-mastigophore; N, basitrich-1; O, basitrich-2; P, S-basitrich; Q, microbasic *p*-mastigophore; R, microbasic *p*-mastigophore. Scale Bar = 20 μm.

endocoelic, opaque, tan to white, approximately 0.5 mm tall. Fosse deep. Pedal disc adherent, roughly circular in outline, paler in color than distal column.

Oral disc and tentacles: Oral disc diameter of expanded individuals slightly greater than pedal disc diameter. center of dic elevated into an oral cone that bears mouth; mouth elongate along directive axis, pale gray to rosy pink in life. Oral disc with opaque marks; marks grouped into six wedge-shaped zones or forming a stellate pattern of concentric, lighter and darker stripes (Fig. 2D, E); pattern fades in preservation. Tentacles slender, marginal, conical, shorter than oral disc diameter: approximately 4 mm long in an expanded preserved individual; innermost tentacles slightly longer than outermost tentacles. Tentacles number 34–80, in three to five cycles. In life, tentacles translucent, typically with opaque white base and cross-bars on oral surface (Fig. 2D, E). Circular muscles of tentacles endodermal, longitudinal muscles ectodermal. Zooxanthellae in endoderm.

Marginal sphincter muscle: Endodermal, circumscribed-pinnate, pedunculate, asymmetrical, with closely spaced, highly branched mesogleal processes (Fig. 6C).

Mesenteries and internal anatomy: Actinopharynx one-half to two-thirds length of column, with two aborally prolonged siphonoglyphs each attached to a pair of directive mesenteries. Marginal stoma slightly larger than oral stoma. Mesenteries in 24–48 pairs, arranged hexamerously into three to five cycles, same number proximally and distally. Mesenteries of first three cycles typically perfect, those of fourth cycle imperfect. All perfect mesenteries, including directives, fertile, each typically bears both male and female gametes (Fig. 6D). Mesenteries of specimens that contain many brooded young typically lack gametic tissue. Zooxanthellae more numerous in endoderm of column than in that of mesenteries. A specimen may contain as many as nine brooded young; brooded young up to 2 mm long, with an oral disc diameter of 1 mm, and as many as 20 tentacles. Largest brooded young zooxanthellate, with small endocoelic verrucae and marginal projections.

Mesenterial retractor muscles diffuse-restricted; retractor typically abuts parietal muscle pennon (Fig. 6E). Parietobasilar muscles strong, each with a broad pennon and many short, thick, lateral processes. Parietal muscle may span as much as half the distance between the column and the free edge of the mesentery. Basilar muscles strong (Fig. 6B).

Cnidom: Spirocysts, basitrichs, heterotrichs, holotrichs, microbasic *p*-amastigophores, microbasic *p*-mastigophores. Sizes

Table 2.—Cnidae of *Anthopleura atodai*. Letter refer to Fig. 5. Sizes are given as ranges of length and width; measurements of exceptionally large or small capsules are in parentheses. "*N*" is the number of specimens examined containing that type of cnidae, "*n*" is the number of capsules measured, including data from holotype. Data for holotype (CMNH-ZG64) are given in separate column.

Location	Type of cnida	*N*	*n*	Size (μm)	*Holotype* (*CMNH-ZG64*) Range (Mean/*SD*)
Tentacle	Spirocyst (A)	4/4	99	15.0–29.8 × 1.8–4.1	22.0–28.5 (25.2/1.63) × 2.5–4.1 (3.0/0.32), *n* = 20
	Basitrich-1 (B)	4/4	18	9.5–13.2 × 1.5–2.3	10.0–13.2 (11.4/11.7) × 2.0–2.1 (2.0/0.05), *n* = 5
	Basitrich-2 (C)	4/4	118	15.2–23.0 × 1.9–2.8	18.2–23.0 (25.9/1.23) × 1.9–2.5 (2.1/0.14), *n* = 21
Acrorhagi	Spirocyst (D)	4/4	66	14.8–33.9 × 2.0–3.8	20.0–33.3 (25.9/3.48) × 2.0–3.0 (2.4/0.42), *n* = 10
	Basitrich (E)	4/4	29	10.8–20.6 × 1.6–2.3	15.2–16.0 (15.6/0.57) × 2.0–2.3 (2.2/0.21), *n* = 2
	Holotrich (F, G)	4/4	266	20.3–48.2 × 2.1–5.8	30.0–42.0 (36.9/3.12) × 3.0–5.0 (3.9/0.50), *n* = 42
Distal column	Basitrich (H)	3/3	84	12.1–17.8 × 1.7–2.6	13.0–16.7 (14.6/0.87) × 2.0–2.2 (2.0/0.06), *n* = 15
Proximal column	Basitrich-1 (H)	4/4	121	9.0–18.8 × 1.3–2.6	10.5–16.3 (14.3/1.65) × 1.8–2.5 (2.0/0.16), *n* = 20
	S-basitrich (I)	4/4	19	21.0–60.9 × 0.9–2.2	21.0–26.0 (23.5/3.53) × 1.0, *n* = 3
	Heterotrich (J)	4/4	71	14.5–19.8 × 2.8–4.1	14.5–18.0 (16.5/1.08) × 3.9–3.9 (3.5/0.33), *n* = 10
Pharynx	Basitrich-1 (K)	4/4	36	11.7-21.3 × 1.6–2.2	18.0–21.3 (15.3/1.03) × 1.8–2.1 (2.0/0.8), *n* = 10
	Basitrich-2 (L)	4/4	103	22.0–28.2 × 1.9–3.2	22.0–28.2 (24.9/0.48) × 2.0–2.8 (2.3/0.27), *n* = 20
	Microbasic *p*-amastigophore (M)	4/4	110	15.2–26.5 × 3.2–5.6	18.0–21.3 (19.8/1.03) × 4.0–5.2 (4.6/0.40), *n* = 20
Filament	Basitrich-1 (N)	4/4	59	11.0–20.1 × 1.8–2.6	14.0–17.0 (15.3/0.46) × 1.8–2.1 (2.0/0.09), *n* = 15
	Basitrich-2 (N)	4/4	110	21.0–28.4 × 2.9–4.6	21.5–25.5 (24.2/11.9) × 3.2–4.0 (3.6/0.27), *n* = 20
	S-basitrich (S)	4/4	60	24.2–36.7 × 0.9–1.7	28.0–35.5 (31.5/2.35) × 0.9–1.2 (1.0/0.07), *n* = 20
	Microbasic *p*-amastigophore (Q)	4/4	118	17.3–25.0 × 3.9–5.5	20.0–23.0 (21.5/0.99) × 3.9–5.0 (4.4/0.36), *n* = 20
	Microbasic *p*-mastigophore (R)	4/4	74	12.0–22.8 × 2.3–4.9	13.5–18.5 (16.5/1.66 (× 2.8–3.2 (2.9/0.15), *n* = 10

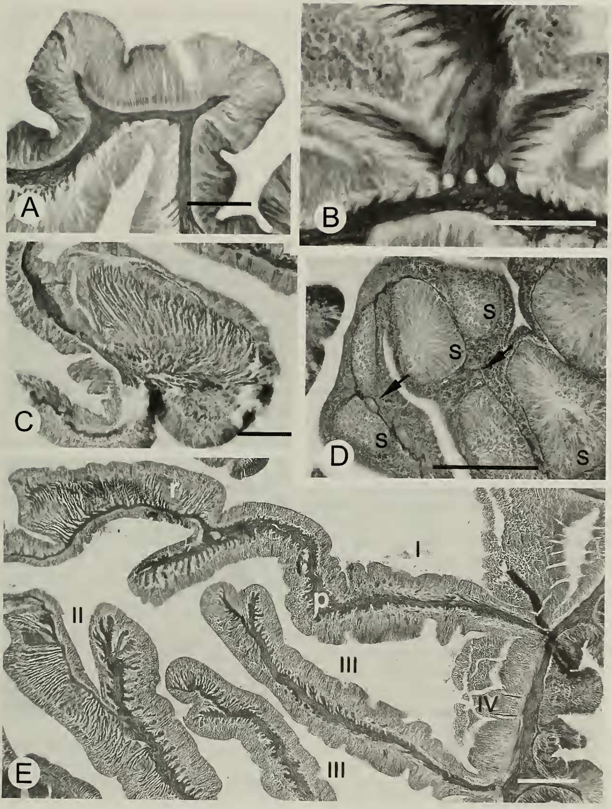

Fig. 6. Internal anatomy and histology of *Anthopleura hermaphroditica.* A, longitudinal section through a verruca; B, longitudinal section through pedal disc showing basilar muscles; C, cross section through sphincter muscle; D, cross section through a mesentery showing both spermatocysts and oocytes; E, cross section through proximal to actinopharynx showing mesenteries of first (I), second (II), third (III), and fourth (IV) cycles. Scale Bars: A = 150 μm; B, C = 100 μm; D = 200 μm; E = 600μm. Abbreviations.—p, parietobasilar muscle; r, retractor muscle; s, spermatocyst. Arrow indicating oocyte.

and distribution of cnidae given in Table 3; cnidae illustrated in Fig. 5.

Distribution and habitat.—Known only from high intertidal zone of Chile.

Discussion

Differential diagnosis.—*Anthopleura atodai* and *A. hermaphroditica* belong to the genus *Anthopleura* by virtue of possessing verrucae, acrorhagi, and columnar heterotrichs. The hermaphroditism and brooding habit of *A. atodai* distinguishes it from other species of *Anthopleura* from waters around Japan, viz. *A. mcmurrichi* Wassilieff, 1908; *A. pacifica* Uchida, 1938; *A. fuscoviridis* Carlgren, 1949; *A. asiatica* Uchida & Muramatsu, 1958; *A. kurogane* Uchida & Muramatsu, 1958; *A. uchidai* England, 1992, and from most other nominal species of *Anthopleura*. It is distinguished from *A. aureoradiata* by the character of verrucae at the lower column and the coloration of the column: in *A. aureoradiata,* the verrucae diminish in size proximally (Parry 1951), and "near the bottom of the column these become mere markings" (Stuckey 1909a: 369); in *A. atodai,* the verrucae increase in size proximally. In *A. aureoradiata,* the coloration of the column differs distally and proximally (Stuckey 1909a, Parry 1951), whereas in *A. atodai,* the coloration of the column is uniform. *Anthopleura atodai* is distinguished from *A. handi* in its hermaphroditism, possession of zooxanthellae, and circumscribed marginal sphincter muscle.

Anthopleura atodai and *A. hermaphroditica* are both hermaphroditic, and brood young internally. However, they are distinguished by number of tentacles, coloration, size of cnidae, and geographical distribution. The maximum number of the tentacles observed in members of *A. atodai* is 62, whereas Carlgren (1899) reported a maximum of 90 in specimens of *A. hermaphroditica.* The column of living specimens of *A. atodai* is bluish-green or brown; in specimens of *A. hermaphroditica,* the column is

Table 3.—Cnidae of *Anthopleura hermaphroditica.* Letters refer to Fig. 5. Sizes are given as a length by width range, in µm; measurements of exceptionally large or small capsules in parentheses. "*N*" is the number of specimens examined containing that type of cnidae, "*n*" is the number of capsules measured. The size range of cnidae for *A. handi,* combined from Dunn (1974) and England (1987) is given for comparison.

Location	Type of cnida	*N*	*n*	Size (µm)	*A. handi*
Tentacle	Spirocyst (A)	6/6	57	15.2–23.9 × 1.8–3.5	11.3–24.3 × 1.4–3.7
	Basitrich-2 (C)	6/6	98	(13.0) 15.0–23.7 × 1.6–3.2	14.1–24.7 × 1.8–3.6
Acrorhagi	Holotrich (F)	5/5	49	32.6–45.8 × 3.0–4.3	29.5–48.2 × 2.6–4.0
	Holotrich (G)	5/5	67	31.3–44.8 × 4.0–7.1	38.9–49.5 × 3.6–4.8
Distal column	Basitrich-1 (H)	5/5	100	9.0–19.7 × 1.0–3.0 (3.8)	9.4–20.7 × 1.8–3.1
Proximal column	Basitrich-1 (H)	5/5	100	(10.0) 12.8–22.0 × 1.5–3.0	9.4–20.7 × 1.8–3.1
	Heterotrich (J)	5/5	81	16.7–24.0 × (2.2) 3.0–4.6	14.2–28.8 (34.2) × 2.7–4.1 (5.7)
Pharynx	Basitrich-1 (K)	4/5	28	12.2–17.9 × 1.3–2.7	11.8–17.7 × 1.8
	Basitrich-2 (L)	5/5	52	21.6–27.3 × 2.1–2.8 (3.5)	15.3–24.8 × 2.4–3.0
	Microbasic *p*-mastigophore (M)	5/5	50	(15.7) 17.1–23.0 × (3.3) 3.7–5.3	16.5–22.7 (24.7) × 3.3–6.2
Filament	Basitrich-1 (N)	5/5	95	10.4–21.8 × 1.5–3.2	8.2–20.0 × 1.8–3.2
	Basitrich-2 (O)	5/5	54	23.7–30.1 × (3.) 3.4–4.9 (5.4)	23.6 × 37.1 (39.1) × 3.2–5.4
	S-basitrich (S)	4/5	11	19.7–29.5 × 1.3–2.0	
	Microbasic *p*-amastigophore (Q)	5/5	59	16.1–27.3 × 2.4–5.6 (5.9)	14.0–21.2 × 3.0–5.8
	Microbasic *p*-mastigophore (R)	3/3	20	14.8–22.8 × 2.3–3.7	10.6–17.7 × 2.4–3.0

Table 4.—Summary of differences in size and distribution of cnidae between *Anthopleura atodai* and *A. hermaphroditica.*

Cnidae type and location	Difference
Tentacle basitrichs	One size class in *A. hermaphroditica*; two distinct classes in *A. atodai*
Acrorhagus holotrichs	Narrower in *A. atodai*
Proximal column heterotrichs	Shorter in *A. atodai*
Proximal column basitrichs	One size class in *A. hermaphroditica;* two distinct classes in *A. atodai*
Filament basitrich-2	Shorter in *A. atodai*

gray or pink. The nematocysts of the tentacles, acrorhagi, column, and filaments further distinguish the two (Table 4).

Taxonomy of Anthopleura hermaphroditica.—The taxonomy of *Anthopleura hermaphroditica* has been confused because of a series of misidentifications and because of a proposed synonymy between *A. hermaphroditica* and *A. handi.* In the original description of the species, as *Bunodes hermaphroditicus,* Carlgren (1899) mentioned two notable features: hermaphroditism and acrorhagi. McMurrich (1904) found specimens of a hermaphroditic actiniid from Chile that had pseudoacrorhagi, rather than true acrorhagi and identified these as *Cribrina hermaphroditica,* changing the generic assignment of Carlgren's species and contesting Carlgren's (1899) assertion that the species had acrorhagi. Carlgren (1927) transferred the species to *Anthopleura,* a genus characterized as having acrorhagi, but maintained that the species he had originally called *Bunodes hermaphroditica* and the specimens described by McMurrich (1904) as *C. hermaphroditica* were the same species. However, after examining additional material from Chile, Carlgren (1959) reversed this opinion, and erected a new species, *B. hermaphroditica,* which he attributed to McMurrich.

Carlgren's (1959) description constitutes a new combination for *C. hermaphroditica* McMurrich 1904, rather than an original description. According to the International Code of Zoological Nomenclature (ICZN 1999: Art. 11.6), the name *C. hermaphroditica* was made available by its subsequent use as valid (e.g., Clubb, 1908), and its authorship dates from its publication by McMurrich (1904) as a synonym of *Bunodes hermaphroditica* (International Code of Zoological Nomenclature: Art. 50.7; ICZN 1999). Therefore, the specimens McMurrich examined constitute the type series for *C. hermaphroditica* McMurrich, 1904; the type specimens of *Bunodes hermaphroditicus* Carlgren, 1899 (SMNH 1177) belong to *Anthopleura* as they have true acrorhagi with holotrichous nematocysts.

The surviving material from the Lund University Chile Expedition includes two recognizable species: *A. hermaphroditica* (Carlgren, 1899) and *Bunodactis hermaphroditica* (McMurrich, 1904). There are many more specimens belonging to *Bunodactis hermaphroditica* than to *A. hermaphroditica*; the difference in number of specimens collected reflects their abundance in the field (V. Häussermann, pers. comm.). Specimens belonging to *Bunodactis hermaphroditica* lack holotrichous nematocysts in the distal column and in the proximal column; both of these features are diagnostic at the level of genus (e.g., England, 1987). Specimens of *Bunodactis hermaphroditica* have more prominent verrucae than specimens of *A. hermaphroditica,* especially proximally.

England (1987) suggested that *A. hermaphroditica* might be synonymous with *A. handi.* We disagree with this proposition of synonymy because *A. hermaphroditica* and *A. handi* differ in several important respects. Most importantly, members these two species differ in key life history features: members of *A. hermaphroditica* are hermaphroditic and zooxanthellate, members of *A. handi* are gonochoric and azooxanthellate. Furthermore, the basitrichs in both the distal and proximal column are larger in members of *A. handi* than in members of *A. hermaphroditica.* Finally, there is a considerable disparity in the geographic range and habitat of the two species: *A. handi* is found in the tropical Indo-Pacific around Malaysia, Singapore, and New Guinea (Dunn 1978, 1982b; England 1987; Fautin 1988); *A. hermaphroditica* is restricted to cold waters of the western Pacific (Carlgren 1899, 1959).

Biology of Anthopleura atodai.—*Anthopleura atodai* clearly corresponds to Atoda's *Anthopleura* sp.: the two have identical distributions, life history, and coloration. All specimens examined, regardless of size, were simultaneously hermaphroditic. In actiniarians, hermaphroditism is unexpectedly rare (Shick 1991) in view of the "low density model" of Ghiselin (1969). Among hermaphrodites, simultaneous hermaphroditsm is the most common mode; known exceptions include the protandrous hermaphrodite *Sicyopis* (= *Kadosactis) commensalis* (Gravier, 1918) and the gynodioecious species *Epiactis prolifera* (Verrill, 1869) and *Cereus pedunculata (*Pennant, 1777) (see Bronsdon et al. 1993, Dunn 1975, Rossi 1971).

The reproductive biology of *A. atodai* remains ambiguous. Isomura et al (2003) were unable to find gametogenic tissue in any specimens that they identified as *Anthopleura* sp. sensu Atoda, although they regularly found brooded young. The mesenteries of some specimens bore spherical protuberances proximally that were interpreted to be early stages of the brooded young; from this they inferred that the brooded young were asexually produced (Isomura et al. 2003). None of our results refute an asexual origin for the brooded young. However, our finding of fertile specimens from the study site of Isomura et al. (2003), including those that contained both gametes and brooded young (e.g., Fig. 4A), indicates that the species is not exclusively asexual, and lends support to the contention by Isomura et al. (2003) that the Mutsu Bay population is remarkable in lacking fertile individuals. In general, the gametes and the gametogenic region are small in *A. atodai,* making it possible that Isomura et al. (2003) overlooked them in the specimens they examined. The presence of gametes does not rule out an asexual origin for the brooded young; some species of *Actinia* have both gametes and asexually produced young in their enteron (Yanagi et al., 1999). Therefore, further investigation is necessary to definitively demonstrate the asexual origin of the brooded young and to clarify reproductive ecology of *A. atodai.*

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